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14. ABSTRACT
We examined the motion encoding characteristics of gyroscopic sensors implicated in the flight control systems of insects. These included antennae of moths and the halteres of large craneflies, two structures that encode the Coriolis forces associated with body rotations during aerial maneuvers in insects. Importantly, no prior research program has explored how the structural dynamics of such gyroscopes interact with motions to provide tunable encoding characteristics. Through both neurobiological and biomechanical approaches we showed how rotational body motions interact with the three-dimensional bending characteristics of biological gyroscopes. We used a combination of neuro-physiological and neuro-anatomical studies to show how the nervous system encodes gyroscopic information. It does so with extremely high precision in the range that is relevant for Coriolis force sensing. This one year research program culminated in a *Science* paper, a variety of news articles, and several publications and presentations at scientific meetings. To our knowledge this is the first successful study of the neural processing of gyroscopic forces in any living creature.

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Abstract

We examined the motion encoding characteristics of gyroscopic sensors implicated in the flight control systems of insects. These included antennae of moths and the halteres of large craneflies, two structures that encode the Coriolis forces associated with body rotations during aerial maneuvers in insects. Importantly, no prior research program has explored how the structural dynamics of such gyroscopes interact with motions to provide tunable encoding characteristics. Through a combination of neurobiological and biomechanical approaches we showed how rotational body motions interact with the three-dimensional bending characteristics of biological gyroscopes. We used finite element analyses, mechanical testing and motion-tracking with digital videography to explore how such gyroscopes encode three dimensional rotational motions and furthermore, how tunable compliance of vibrating structure gyroscopes (VSGs) may be utilized to precisely control their sensory bias. We used a combination of neuro-physiological and neuro-anatomical studies to show how the nervous system encodes gyroscopic information. It does so with extremely high precision in the range that is relevant for Coriolis force sensing. This **one year** research program culminated in a *Science* paper, a variety of news articles, and several presentations at scientific meetings. To our knowledge this is the first successful study of the neural processing of gyroscopic forces in any living creature.

Introduction:

To achieve a fine motion control, moving systems require a diverse array of sensors to inform them of their motion. Robotic devices, autonomous flight vehicles, and terrestrial, aquatic and flying animals all rely on crucial feedback from several sensory modalities for locomotion control. In vertebrates, the visual and vestibular systems act in concert with proprioceptive sensors to coordinate the flow of information for movement control. Visual sensing has often been argued to be the most powerful controller of flight systems, particularly in insects (Land and Collett, 1974; Collett and Land, 1975). Yet despite the great capacity of visual systems for tracking complex motions and regulating flight they suffer from one critical limitation: the processing time of insect visual systems is often quite slow relative to the natural perturbations that typically influence the flight path. For example, in most insects, the responses of visual neurons in the lobular plate (insect optic lobe) to external motion stimuli are on the order of 50 to 100 ms (hawk moth, Manduca sexta, Theobald, 2004; blowfly, Calliphora (Warzecha and Egelhaaf, 2000),). The delay between an eventual motor response to visual stimuli may be even greater in the case of crepuscular or nocturnal insects which fly under very low light conditions Because each wing stroke lasts approximately 40 ms, such delays are problematic for rapid course correction. Indeed three dimensional motion control likely requires sensory information processing over much faster timescales than the 50-200 ms delays associated with insect visual information processing (see control theoretic work in prep by (Dickson and Dickinson, 2004), Hedrick and Daniel, 2005 (SICB)).

In most organisms including insects, rapid responses e.g. escape reflexes are typically mediated by mechanosensors. For example, moths often perform rapid escape maneuvers from predatory bats through mechanosensory-mediation of auditory responses. However, these responses involve little more than a quick evasion of the approaching bats *via* a rapid cessation of flight. A finer control of flight course, on the other hand, requires more sophisticated mechanosensory organs such as the halteres in Dipteran insects, which monitor the flight course on a stroke-to-stroke basis. These dumb-bell shaped structures, derived from a reduction in the hindwings, are actively oscillated out of phase with the beating wings. Imbued with a rich set of strain sensors, halteres have been shown to be exceptional gyroscopic sensors (Pringle, 1948; Nalbach, 1994). Indeed the pioneering work by Pringle (1948) and Nalbach and Hengstenberg (1994) and recent work by Dickinson and his co-workers (Fayyazuddin and Dickinson, 1996; Chan et al., 1998; Dickinson, 1999; Sherman and Dickinson, 2003) shows that fly halteres are capable of rapidly encoding subtle lateral displacements of the halteres due to Coriolis forces. Moreover, it has been shown that the haltere motor apparatus receives direct input from the visual system and thus also mediates the visuo-motor response of the flight muscles to external perturbations (Chan et al., 1998). Despite the great promise of using halteres as model systems for gyroscopic control devices, remarkably little is known about their neurobiological and biomechanical characteristics. Moreover, while halteres are heralded as the insect vestibular system, there remains the unanswered and tantalizing question of how non-Dipteran insects (which do not possess halteres) encode Coriolis forces or otherwise achieve course control. Might not the host of insect species that do not have halteres require similar sensory information encoding for effective flight control? Indeed, it is quite surprising to note the paucity of studies focusing on alternative gyroscopes.

What we accomplished

We embarked on a multi-pronged research project that asked (1) how biological gyroscopes (bio-gyros) respond to Coriolis forces and (2) how those forces are encoded by the nervous system. We used a combination of biomechanical and neurophysiological approaches to show that moth antennae act as bio-gryos and have neural processes that extend into their flight motor control. The two key findings are that

(1) Antennal mechanosensors are indeed gyroscopic organs capable of encoding Coriolis forces. The figure below (from Sane et al, 2007) captures the essential details of this conclusion. In panel (A) we show that the antennal mechanosensory cells respond to natural motion stimuli (dark line in A is a 1 degree motion) as indicated by the raster plot of neuronal spiking beneath the stimulus trace (three animals). Panel (B) shows a stimulus frequency sweep with the resulting neuronal spiking. Beneath the spike trace is the Gaussian convolved firing rate that has a strong linear response at the frequency that is critical for encoding the Coriolis forces (about 50 Hz). Panel (C) shows a gain and phase plot for the firing rate. This too shows a strong responsiveness at the critical frequency of 50 Hz. Finally, panel (D) shows two neurons that encode mechanosensory information relevant to Coriolis forces. These project directly into the motor control portion of the brain.

QuickTime™ and a
TIFF (Uncompressed) decompressor
are needed to see this picture.

Simi

(2) The biomechanical properties of compliant gyroscopes suggest that they can be tuned to respond to particular motions (Daniel et al, 2007). In a series of studies we have quantified the mechanical properties of halteres and antennae (see

abstracts below). Towards this end, we have developed finite element models of a vibrating structural gyroscope (Myhrvold et al, 2007 *in prep*; Fox et al, 2007 *in prep*). Here we report on one very simplified version of these models– a thin walled, tapered, hollow cylinder subject to periodic angular velocity in one plane with a simultaneous constant rotational velocity in an orthogonal plane. We used the geometry, frequencies and amplitudes reported in Sane et al (2007) for moth antennae to guide our simulations. Simulations were run for a variety of compliances and motions to explore the possibility of tuning for these structures.

Several important results emerge from our analyses (see http://faculty.washington.edu/danielt). First, as would be expected from simple beam theory, the strains and stresses are largest near the base of this oscillating and spinning structure (Figure 2 below). Interestingly, we also note that the greatest concentration of strain sensors (campaniform sensilla) in both halteres and antennae occurs at their proximal base. This suggests that sensilla are located in regions of greatest strain.

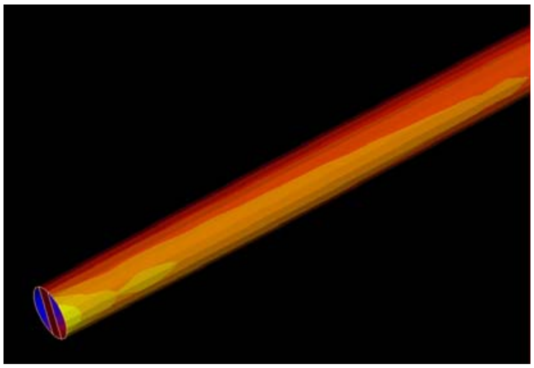

Figure 2. The pattern of stress in a finite element model shows that peak values occur at the base of a model gyroscope (hollow cylinder). Bright yellow corresponds to a tensile stress of approximately 1 MPa. The upper figure is a view of the entire model and an expanded view is shown immediately below.

A second result is that the temporal pattern of strain contains the characteristic twice-frequency signature of the Coriolis force that is expected for vibrating structures subject to angular precession. We show this by plotting below (Figure 3) the power spectrum of a component of the strain tensor (e_{22})

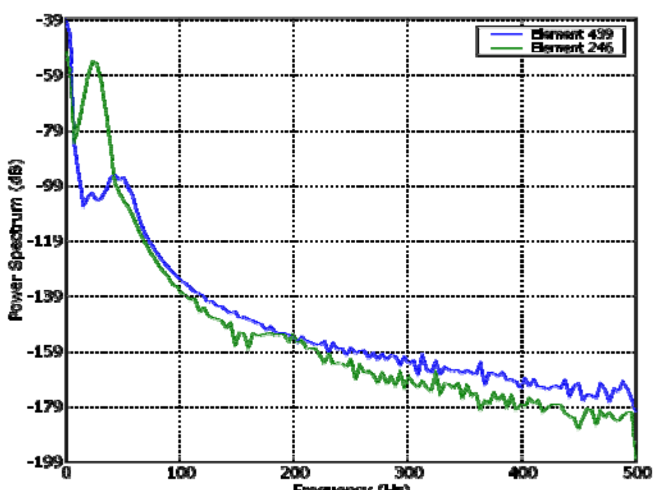

Figure 2. The power spectrum of a component of the strain tensor for two locations. One on the dorsal aspect of the structure (green) and the other on the lateral aspect (blue). Note that there is a component at the driving frequency (25 Hz) and the Coriolis signature (50 Hz).

Finally our simulations suggest that gyroscopes can be tuned to best detect rotational motions by adjusting their vibrational driving motions along with their mechanical properties. In simulations summarized below (Figure 4) we show that peak strains and stresses occur at unique combinations of driving frequency, rotational velocity and mechanical properties. In the three panels below we plot the peak value of the stress tensor (red = 1 MPa) as a function of the vibrational driving frequency (vertical axis) the rotational velocity (horizonal axis) and three values of the stiffiness of the cuticle. In the upper panel we use values for cuticle stiffness that are one tenth (upper panel), equal to (middle panel) or ten times (lower panel) that reported for insect cuticle (1 GPa). The location of a unique peak for strain suggests that biological gyroscopes can be mechanically tuned to sense specific ranges of rotational motion

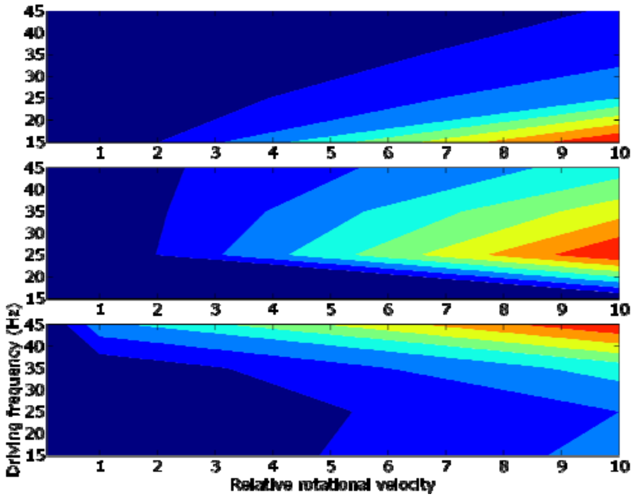

Figure 4. The peak value of the stress tensor (red = 1 MPa, dark blue = 0 MPa) is plotted against driving frequency and rotational velocity for three values of the stiffness of insect cuticle (0.1 GPa: upper panel, 1 GPa: middle panel, 10 GPa: lower panel).

These computational analyses point to several general design principles for biological gyroscopes. First there are complex three dimensional patterns of strain when these structures are subject to Coriolis forces. Additionally, those strains are dominantly associated with the base of the structure where there is the greatest concentration of strain sensors. Moreover, the mechanical properties of these structures can be tuned to encode a particular range of motions.

Future possibilities

(1) Compliant wings may act as gyroscopes? Towards the end of the funding period, we embarked on a parallel set of studies that asked how the insect precursors of halteres (strain sensors in hind wings) might also serve as potential sensors of gyroscopic forces. Wings of all insects are embued with a rich set of strain sensors whose function remains enigmatic. We recorded from the sensory nerve at the base of the wing and found that those strain sensors there behave identically to ones found at the base of antennae and halteres. They respond to deformations within a few milliseconds of deformation, they encode linearly in the frequency domain that is relevant for measuring, and do so with incredible precision (> 95% accuracy in phase locking as measured by vector strength).

(2) Might compliance in wings provide a novel aerodynamic lift mechanism? Because we became very interested in the bending dynamics of wings, we pursued one additional avenue of research that focused on the natural motions of highly compliant wings (see abstracts by Mountcastle and Daniel below). We found large bending waves propagate in the chordwise direction for freely flying animals. Moreover, particle image velocimety of robotically actuated wings showed that these waves profoundly affect the nature of the flow, leading to nearly a 30% increase in momentum flux compared to wings of the same mass that were stiffened.

Taken together, we feel that there is a promising new avenue of research and that the one funding we received has yielded significant results.

Publications and abstracts resulting from the research

(we do not list here the popular press articles about our work, but would be happy to provide it!).

Daniel, T.L., Dieudonne, A., Fox, J., Myhrvold, C., Sane, S., and Wark, B. (2007) The inertial guidance systems in insects: from neurobiology to the structural mechanics of biological gyroscopes. Proceeding of the 2007 Institute of Navigation Conference.

Sane, S.P., Dieudonne, A, Willis, M.A., and Daniel, T.L. (2007) Antennal mechanical sensors mediate flight control in Lepidoptera. *Science*. 315:863-866

Alexander, R.McN. Antennae as gryoscopes. (2007). *Science* 315:771-772.

Abstracts

Geiger, M., Fox, J.L., Myhrvold, C.A., and Daniel, T.L. 2008. Morphological and mechanical asymmetry in a biological gryoscope. Society of Integrative and Comparative Biology Annual Meetings. San Antonio, TX

Hinterwirth, A. and Daniel, T.L. 2008. Multiple inputs and multiple outputs mediate flight control in Manduca sexta. Society of Integrative and Comparative Biology Annual Meetings. San Antonio, TX

Fox, J.L. and Daniel, T.L. 2008. Endoding properties of haltere mechanoreceptors. Society of Integrative and Comparative Biology Annual Meetings. San Antonio, TX

Fox, J.L. and Daniel, T.L. 2007. Sensory encoding in the gyroscopic halteres of the crane fly *Holorusia*. Eighth International Congress of Neuroethology, Vancouver, Canada.

Crook, J.D., Fox, J.L., Dieudonne, A. and Daniel, T.L. 2007. Encoding properiteis of campaniform sensilla on the wing of *Manduca sexta*. Eighth International Congress of Neuroethology, Vancouver, Canada.

Dieudonne, A., Sane, S., Myhrvold, C.A., Fairhall, A., and Daniel, T.L. 2007. The encoding properties of gyroscopic sensors in hawkmoth antennae. Eighth International Congress of Neuroethology, Vancouver, Canada.

Myhrvold, C.A., Fox, J.L., Sane, S.P. and Daniel, T.L. 2008. Strain patterns on an antenna: are moth antennae tuned? Society of Integrative and Comparative Biology Annual Meetings. Orlando, FL

Sane, S.P., Dieudonne, A. and Daniel, T.L. 2007. Role of antennae in insect flight control. Society of Integrative and Comparative Biology Annual Meetings. Orlando, FL

Fox, J.L. Myhrvold, C.A., and Daniel, T.L. 2007. Sensory encoding in the gyroscopic halters of the crane fly Holursia rubignosa. Society of Integrative and Comparative Biology Annual Meetings. Orlando, FL